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Abstract: Behavioral responses of animals to direct predator cues (DPCs; e.g., urine) are common and may improve their survival. We investigated wild meerkat (Suricata suricatta) responses to DPCs by taking an experimental approach. When meerkats encounter a DPC they often recruit group members by emitting a call type, which causes the group members to interrupt foraging and approach the caller. The aim of this study was to identify the qualities of olfactory predator cues, which affect the strength of response by meerkats, and determine the benefits of responses to such cues. Experimental exposure to dog (Canis lupus) urine as a DPC revealed that the recruited individuals increased vigilance to fresh urine in comparison to older urine, whereas a higher quantity of urine did not induce such an effect. Both freshness and higher quantities increased the proportion of group members recruited. These results indicate that recruitment might play a crucial role in correctly assessing the current level of danger and that recruiting might facilitate group decision making. To test the prediction that the reaction to a DPC enhances early predator response, we presented a DPC of a predator and a control cue of a herbivore, and each time simultaneously moved a full-mounted caracal (Caracal caracal) in the vicinity of the group. Meerkats responded earlier to the caracal when the DPC was presented, indicating that the response to a DPC facilitates predator response and that they use information from the cue that reliably reflects the risk in the current moment.

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The effects of recruitment to direct predator cues on predator responses in meerkats

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Behavioral responses of animals to direct predator cues (DPCs; e.g., urine) are common and may improve their survival. We investigated wild meerkat (*Suricata suricatta*) responses to DPCs by taking an experimental approach. When meerkats encounter a DPC they often recruit group members by emitting a call type, which causes the group members to interrupt foraging and approach the caller. The aim of this study was to identify the qualities of olfactory predator cues, which affect the strength of response by meerkats, and determine the benefits of responses to such cues. Experimental exposure to dog (*Canis lupus*) urine as a DPC revealed that the recruited individuals increased vigilance to fresh urine in comparison to older urine, whereas a higher quantity of urine did not induce such an effect. Both freshness and higher quantities increased the proportion of group members recruited. These results indicate that recruitment might play a crucial role in correctly assessing the current level of danger and that recruiting might facilitate group decision making. To test the prediction that the reaction to a DPC enhances early predator response, we presented a DPC of a predator and a control cue of a herbivore, and each time simultaneously moved a full-mounted caracal (*Caracal caracal*) in the vicinity of the group. Meerkats responded earlier to the caracal when the DPC was presented, indicating that the response to a DPC facilitates predator response and that they use information from the cue that reliably reflects the risk in the current moment. *Key words:* direct predator cues, meerkats, olfactory cues, predator detection, predator odor, recruitment, vigilance. *[Behav Ecol]*

INTRODUCTION

Many animals face a trade-off between foraging and predator avoidance (Lima and Dill 1990; Verdolin 2006; Morrison 2011). It is therefore highly beneficial for individuals to assess the actual predation risk and adjust their antipredator investment according to the perceived danger. Evidence for this adjustment has been demonstrated in a number of species (Hilton et al. 1999; Barta et al. 2004; Devereux et al. 2006). Theoretical models support the assumption that changes in foraging behavior help to minimize predator exposure and encounter rate (Lima and Dill 1990; Lima 1998) and experimental evidence suggests that vigilant individuals spot approaching predators at further distances than foraging ones (Lima and Bednekoff 1999) and are probably less vulnerable to predation (Fitzgibbon 1989; Krause and Godin 1996; Hilton et al. 1999).

Direct predator cues (DPCs) are inadvertently left calling cards (e.g., urine, feces, and hair, heterospecific alarm calls) which can be used as indicators of nearby predators and magnified predation risk. Consequently, DPC recognition likely allows an individual to assess the current level of danger. Mammals respond to predator odors with changes in spatial activity, decreased feeding rate, and increased vigilance (Berger et al. 2001; Apfelbach et al. 2005; Blumstein et al. 2008) and similar responses to DPC are widespread in different taxonomic groups (birds: Roth et al. 2008; Ridley et al. 2010, fish: Wisenden 2000; Brown 2003; Ward and Mehner 2010, reptiles: Ito and Mori 2010, invertebrates: Foust et al. 2001; Gherardi et al. 2011, for a review see: Kats and Dill 1998). Although behavioral changes are well documented and are frequently assumed to be adaptive, there currently exists little experimental evidence demonstrating that reactions to DPCs actually improve an animal's ability to avoid predator encounters—a response which would have direct fitness benefits to the prey.

Moreover, it is of advantage for prey species to be able to assess the reliability of DPCs as old cues are probably not associated with high-risk situations. Such adjustment has been shown for the wolf spider (*Paradosa milvina*) and the brushtail possum (*Trichosurus vulpecula*), which react more strongly to a fresh than an old cue of their predator (Barnes et al. 2002; Kirmani et al. 2010). Other qualities of the cue, which are also highly variable, may be less reliable for assessing the current predation risk, such as the amount of predator urine deposited. Variation in the amount of urine deposited from carnivores can be caused by different ways of urinating that may serve different functions (e.g., fox: Jorgenson et al. 1978, feral cat: Natoli 1985, and domestic dog: Hart 1974). Carnivores mark their territory by spraying, a behavior where often small amounts of urine are excreted, or excrete larger amounts without dispersing.

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As expected, studies also found strong sex-dependent variation in the use of these techniques in carnivores (Hart 1974; Liberg 1980). Hence, the quantity of a urine deposit might be an unreliable quality for risk assessment. Animals using DPC for risk assessment should therefore be sensitive to those qualities, which signal risk reliably.

A common assumption regarding DPCs is that various behavioral adaptations to these cues, such as suppressed breeding (Fuelling and Halle 2004), reduced activity, higher giving-up densities (Apfelbach et al. 2005), or increased vigilance (Monclus et al. 2005, 2006), lead to increased prey survival. One mechanism that can increase survival chances of prey species is early predator detection because detected predators may abandon the hunt (Fitzgibbon 1989; Lingle and Wilson 2001) or because successful flight response of prey is facilitated (Krause and Godin 1996).

We used a combined approach of observational data and experimental manipulation of DPC encounters in wild, free-living meerkats (*Suricata suricatta*) to investigate which cue qualities affect the response to DPCs and how meerkats benefit from attending to DPCs. Meerkats are small, cooperatively breeding carnivores living in Southern Africa. They face high predation pressure by aerial and terrestrial predators (Clutton-Brock et al. 1999a) and have developed a coordinated sentinel (Manser 1999; Clutton-Brock et al. 1999b) and vigilance system (Townsend et al. 2011). The study population occupies farmland, where encounters with domestic animals including predators like domestic dogs (*Canis lupus*) and cats (*Felis catus*) have been documented (Kalahari Meerkat Project (KMP), long-term database, unpublished data). In response to predators they employ an elaborate spectrum of alarm calls encoding referential as well as motivational information (Manser et al. 2002). When a meerkat encounters a DPC such as cat, dog, caracal, or bat-eared fox urine *(Otocyon megalotis)*, feces, or hair, it reacts immediately by emitting recruitment calls, whereas terrestrial alarm calls are emitted when a standing or moving predator on the ground is spotted (Manser 2001). In response to recruitment calls, the rest of the group interrupts foraging and approaches the caller to inspect the cue (Manser et al. 2001). This gathering typically results in the group moving away from the cue to a different area before their onset of foraging again, or the group resuming foraging after several minutes in the vicinity of the cue.

We analyzed the natural frequency of recruitment events, and in the same population exposed meerkats to dog urine of different age and containing different quantities of urine. Finally, we tested experimentally if the reaction meerkats show toward a DPC leads to faster predator response. We predicted that meerkats should be sensitive to those qualities of DPC, which have the potential to reliably convey information to the receivers about risk, such as cue freshness, but not to qualities, which do not allow risk assessment, such as the amount of urine. Furthermore, we expected that DPC encounters facilitate the response of meerkats to live predators by decreasing latency to emit an alarm call.

MATERIALS AND METHODS

The study animals

Observations and experiments were performed with wild meerkats at the KMP, in the Kuruman River Reserve and on surrounding farm land in South Africa. Observations on recruitment behavior were analyzed for the period of January–December 2007. Experiments were conducted in August and September 2005, and from August 2006 to January 2007 (urine exposure experiment) and between June and August 2008 (predator detection experiment). The study site is located 30 km west of Van Zylsrus, in the southern part of the Kalahari desert (see Clutton-Brock et al. 1999a for detailed ecological description). The groups were habituated to human presence (closer than 1 m) and all group members were individually identified by unique dye marks (Jordan et al. 2007). In total, 38 DPC presentations in 12 groups (group size: median = 20; range = 5–32) were conducted for the urine exposure experiment and 14 cue presentations in 7 groups (group size: median = 12; range = 5–17) for the predator detection experiment.

The long-term observational data

To estimate the natural encounter rate of DPCs, we analyzed 1 year of adlib data from the long-term data set of the KMP in 11 groups. Each group had been followed every week on at least 3–4 days for 2–4 h during the morning foraging sessions and on 2–4 days during 1–2 h in the afternoon foraging sessions, resulting in 6268 h of observation (on average 570 per group; range 401–627 h). According to the KMP protocol (Version 2006), every predator encounter and encounter of DPC or meerkat feces/scent that caused mobbing, inspection, or recruitment was recorded. In most cases, we could not identify the actual cue but in other observations the meerkats behaved in similar manners regardless of whether the cue was secretions from glands, feces, carcasses, or hair hidden in the vegetation. From these observations we calculated the encounter rate resulting in recruitment to mob an alive predator, and inspect a scent (unidentified or identified) per observation hour per group.

The effect of age and quantity of a DPC

In our experiments, we used DPCs from terrestrial predators that had previously been shown to elicit a recruitment response by meerkats (Manser 2001; Graw and Manser 2007). We used dog urine to test whether meerkats show a different response toward fresh and old urine or to different quantities (1 or 4 ml) of DPC. The dog urine was either added to the sand 5–10 min before the presentation (below referred to as fresh urine) or 24 h before the presentation and left outside exposed to the sun and outdoor temperature (referred to as old urine). To test whether the quantity of dog urine had an influence we presented samples of sand with fresh dog urine of the according amount. These experiments were conducted in a randomized order. The dog urine was presented to 1 randomly chosen adult focal individual and the response was filmed with a camera (Sony Digital Camcorder HDR-HC5). In case the focal individual did not react, the dog urine was presented to other randomly chosen individuals until an individual sniffed on the cue. The samples of sand with the dog urine were presented on cardboard (8×12 cm) allowing easy and consistent handling with the sample. All the experiments were conducted when the group was foraging. In case of any predator alarm or other disturbances the experiments were postponed until the group was foraging uninterrupted for at least 15 min. To avoid habituation we left a minimum interval of 1 week between experimental presentations within the same group.

In total, we conducted 38 cue presentations in 12 different meerkat groups and averaged measures from the same group if the same stimulus type was presented. This resulted in a sample size of 28 cue presentations. We modeled the proportion of group members recruited, average vigilance, and the latency

to resume foraging (time period between first recruitment call and foraging onset afterwards) with linear mixed effect models assuming normal error structure with identity link function. These analyses were carried out in R, Version 2.14.0 (R Development Core Team 2011) using the package lme4 (Bates et al. 2011). The response variables were log or square root transformed and subsequently did not differ from a normal distribution. To analyze the influence of cue age and cue quantity on the proportion of group members recruited we included both as fixed factors with 2 levels each (fresh/old and 1 ml/4 ml) and the group identity as a random factor. Examination of the Akaike information criterion (AIC) (Table 3) suggested that all terms should be retained in the final model. When modeling vigilance and the latency to resume foraging, we included the same fixed and random effects as in the previous model and additionally included the number of individuals recruited as a covariate. We then simplified models and dropped terms if it decreased the AIC (Table 3) until no more terms could be dropped. Terms which were not included in the final model are displayed in Table 2 with the values before they were excluded in the model selection process. Preliminary data analysis suggested that group size is not correlated with the proportion of group members recruited (Spearman, $N = 28$, $P = 0.85$), with vigilance (Spearman, $N = 25$, $P = 0.98$) and that the reproductive state of groups (presence of dependent young) does not influence these response variables to predator cues (Lienert 2007). Hence, these factors were disregarded in the model selection process. All figures presented in this paper are based on untransformed raw data.

The caracal detection experiment

Each meerkat group was tested to determine how fast they responded to a terrestrial predator once with a DPC in the experimental treatment and once with the herbivore cue in the control treatment. As predator cue we used cat hair or bat-eared fox fur, which had been stored at −20 °C and defrosted a few hours before presentation. Using the same type of standardized DPC would have been the preferred option, but this was not possible due to practical limitations in access to cues in the field. However, both indicate the presence of a terrestrial predator and previous experiments have shown that these cues elicit qualitatively the same response in meerkats (cf., Manser 2001). As a control cue we used antelope hair (*Oryx oryx*) stored and presented in the same way as the DPC. In the experimental and control treatment we placed the cue in the center of the foraging group. As soon as 1 of the group members inspected the cue, we started to move a full-mounted caracal parallel to the group in an average distance of 78 m (range: 49–142 m, see Table 1). Caracals are sympatric predators and prey on a range of mammals of various sizes from rodents to medium-sized antelopes (Melville et al. 2004). Prior to presentation the dummy predator was hidden behind a camouflage fabric and was therefore invisible to the group. We measured the latency of predator detection defined as the time when the first meerkat began to inspect the cue (sniffing) until the first terrestrial alarm call was given by any of the group members, in response to the mounted caracal being moved. To control for order effects, half of the groups started with the experimental treatment, whereas the other half started with the control treatment.

We standardized, as much as possible, the distance between the group and the caracal, the visibility and the habitat structure in the experimental and control treatments. If impossible, we accepted a larger distance and poorer visibility in the experimental than in the control treatment. This excluded the proximity or the visibility of the predator as an alternative explanation for faster predator detection (Table 1). After an experiment, we took a photo with a digital camera (Konica Minolta Dimage X1) from the presentation spot toward the caracal. The camera was positioned at a standard height of 35 cm, which corresponds to the height of the head of an adult meerkat standing on its hind legs. Later, these photos were shown to 12 naïve human observers, who were asked to score the visibility of the predator on a 3-stage scale (good, medium, and poor). At the time of the presentation, there were no meerkats acting as sentinels (look-out position at least 10 cm above ground) or meerkats emitting sentinel calls (Manser 1999). We analyzed the latency to predator detection between the 2 treatments using an exact Wilcoxon test.

Table 1
Physical conditions for the presentations of DPCs and control cues (Control) in each meerkat group

	Visibility		Distance to predator (m)		Landscape	
Group	DPC	Control	DPC	Control	DPC	Control
KU	Good	Good	142	87	Dunes	Dunes
F	Good	Good	51	49	Flats without bushes	Flats without bushes
D	Medium	Medium	94	95	Flats without bushes	Flats without bushes
AZ	Poor	Medium	93	78	Flats with bushes	Flats with bushes
W	Poor	Medium	80	64	Flats with bushes	Flats without bushes
L	Poor	Medium	90	56	Hills	Hills
CD	Poor	Poor	64	53	Flats with bushes	Flats with bushes

Visibility estimated by naive observers (modal values), distance to the predator in meters measured by a rangefinder, and landscape type in which the experiments were performed are displayed.

RESULTS

Natural occurring recruitment events

In total, the 11 meerkat groups recruited group members 529 times in 6268 h of observation during foraging (range: 36–77 recruitment events per group). This resulted in a recruitment frequency of 1 recruitment per 12.6 ± 0.75 (range: 8.1–15.6) h observation time ($n = 11$ groups). On average 40.6 ± 2.54% were due to a predator that was encountered by 1 of the group members, who used the recruitment calls to initiate mobbing (cf., Graw and Manser 2007). In 53.2 ± 2.82% of the recruitment events, they were elicited by odors that could not be identified. Only 4 ± 0.94% of all recruitment events were elicited by obvious identifiable feces of predators or conspecifics, and the rest (2%) was caused by carcasses, body parts, or artificial objects (e.g., bottles).

Effects of age and quantity of DPC on the recruitment

Presentations of dog urine elicited recruitment calls, which caused other individuals to approach the calling individual in 35 of 38 cases. Not all individuals inspected the cue, even though a standardized distance and way of presentation to the different test animals was kept. However, the probability to inspect the cue

was not dependent on the quality or quantity of the presented cue (fresh/1 ml: 2.63±0.53 times; fresh/4 ml: 1.64±0.48 times; old/4 ml: 1.25±0.57 times; generalized linear mixed model (GLMM), binomial distribution; age: estimate = 0.31±0.54, $P = 0.56$; amount: estimate = 0.42±0.50, $P = 0.39$). In 3 of the cases no individual approached the calling individual despite recruitment calls. On average 45±4 (range: 0–100) % of the group members were recruited. Individuals which were recruited spent on average 22.06±5.5 (range 0–127) s inspecting the cue and scanning the surroundings for predators until the groups after 122±16.0 (range 0–399) s resumed normal foraging activity.

Inspection behavior of the meerkats to the presented dog urine differed depending on the age and the amount of the cue. The proportion of individuals recruited to the cue increased with cue freshness and with cue quantity presented (Table 2, panel a; Figure 1a,1b). However, the time individuals were vigilant after they were recruited and inspected the cue was only enhanced by fresh, but not by larger amounts of urine. Additionally, vigilance time increased when more individuals were recruited to the cue (Tables 2, panel b and 3, panel a; Figure 1c,1d). Finally, the latency to resume foraging was significantly increased by fresh urine and tended to be high when large quantities of urine were presented (GLMM; age: estimate = −5.56±1.9, $P = 0.014$; amount: estimate = 3.66±1.91, $P = 0.05$). However, when controlling for the number of animals which were recruited, neither of these factors explained a significant proportion of variation (Table 2, Figure 1e,1f) and model selection by AIC suggested that the covariate "number of animals recruited" predicted how long a group would interrupt foraging after predator cue encounters and should be retained in the model.

Predator detection experiment

The detection time of the caracal was strongly influenced whether the groups were presented a DPC or a control cue. When the predator cues were presented, the animals inspecting the cue always gave a few or several recruitment calls, whereas when encountering the control cue, they never called (binominal: $P = 0.016$; $N = 7$). This caused the rest of the group to approach the caller in all the cases of the DPC, but never to the control cue (binominal: $P = 0.016$; $N = 7$). The latency to the first alarm call in response to the presented caracal was shorter when the meerkat groups were exposed

Table 2

Model parameters for (a) proportion of the group recruited, (b) vigilance of recruited individuals, and (c) latency to resume foraging

	Estimate	±Standard error	*t*-Value	*P*-value
(a) Proportion of group recruited				
Intercept	**0.26**	**±0.06**	**4.47**	
Age of urine	**−0.23**	**±0.08**	**−2.91**	**0.004**
Amount of urine	**0.2**	**±0.08**	**2.59**	**0.01**
(b) Vigilance of recruited individuals				
Intercept	**1.13**	**±0.41**	**2.75**	
Age of urine	**−1.56**	**±0.37**	**−4.25**	**<0.001**
Number of animals recruited	**0.18**	**±0.03**	**5.25**	**<0.001**
Amount of urine	0.21	±0.42	0.42	0.60
(c) Latency to resume foraging				
Intercept	**4.73**	**±1.18**	**4.01**	
Age of urine	**−1.75**	**±1.28**	**−1.36**	**0.19**
Number of animals recruited	**0.7**	**±0.11**	**6.18**	**<0.001**
Amount of urine	**0.38**	**±1.51**	**0.25**	**0.78**

Final model parameters are displayed in bold. Terms which were not included in the final model are displayed with the *P*-value at which they were excluded from the model.

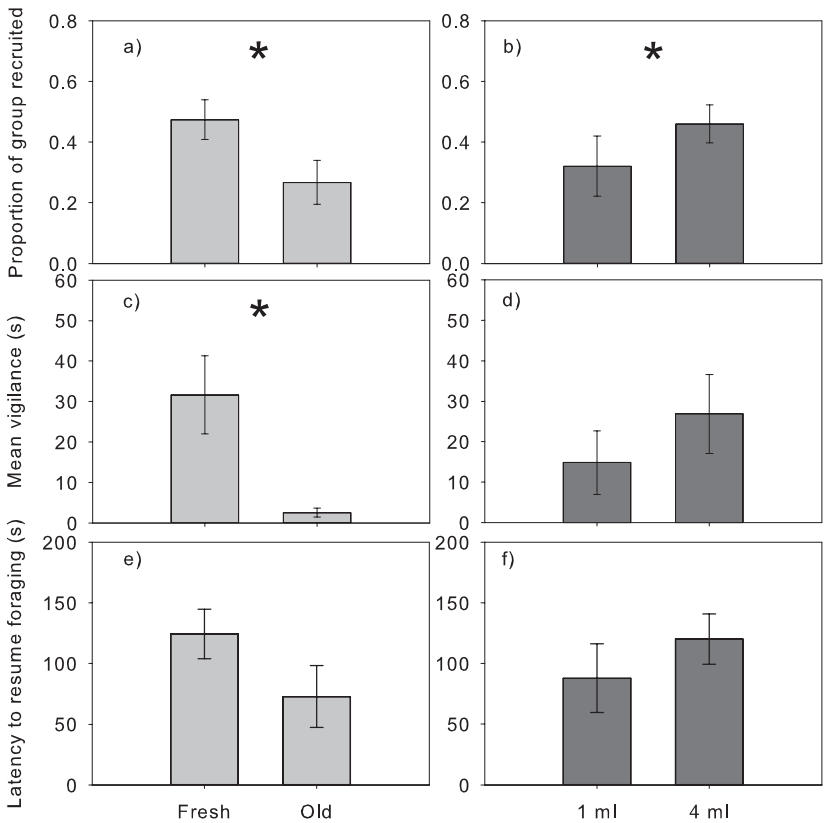

Figure 1
The proportion of the group recruited to dog urine (DPC) presentations (a) and (b), the mean vigilance per individuals in seconds (c) and (d), and the latency to resume foraging (e) and (f) plotted against cue age (a), (c), and (e) and cue quantity (b), (d), and (f). Asterisks indicate statistical significance (see Table 2 for model details).

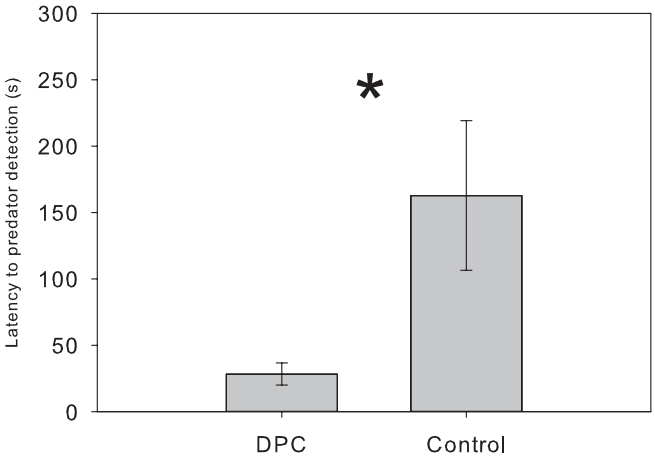

Figure 2
Latency to predator detection (in seconds) by meerkat groups ($N = 7$) after exposure to a DPC or a control cue (Control). Asterisks indicate statistical significance.

to a DPC compared with a control cue (exact Wilcoxon test: $P = 0.02$; $N = 7$; Figure 2). The individual who first emitted the alarm call to the caracal in the DPC treatment was the individual that had encountered the cue first only in 2 groups. In 3 groups it was another individual. For the other experiments ($N = 2$) we were unable to determine the first caller. Only in 1 out of 7 cases the individual closest to the predator alarmed first. In the control treatment, the individual that inspected the cue first was not, in any trial, the individual to emit the alarm call to the caracal first.

DISCUSSION

Response by meerkats related to cue qualities

During foraging trips, meerkats regularly encountered DPCs, to which they typically recruited other group members and inspected it together. Often the whole group interrupted foraging to inspect the cue. In our experimental study, the intensity of the response by meerkats to a DPC depended on the age, but less on the quantity of the cue. Meerkats inspected the cue and scanned their surrounding longer when the cue was fresher, but not when the quantity of the cue was increased. This effect was still present when statistically controlling for the number of recruited individuals, indicating despite the fact that the number of recruited animals predicted vigilance of each individual, cue age also affected vigilance.

Meerkats appeared to assess the enhanced danger of predation indicated by the fresh urine and adjusted their behavior accordingly. The freshness of the cue might indicate that the predator, which had left the cue, was still in the vicinity. Thus, a fresh cue might be a valuable indicator denoting an increased risk of predation in this area, similar to what has been demonstrated experimentally in the wolf spider (Barnes et al. 2002) and brushtail possums (Kirmani et al. 2010).

The presentation of a larger quantity of urine induced the recruitment of a higher proportion of group members, but did not increase individual vigilance or the latency to resume foraging in comparison to the lower quantity. This suggests that the meerkats initially discriminated between lower and higher quantity of the DPC, but then may not have perceived the situation more risky due to higher quantity as observed with fresh urine. By recruiting group members, the reaction of the recruited individuals may help to assess the situation more accurately, yielding benefits associated with group decisions (Conradt and Roper 2007). Such an effect is known from fish, which make faster and more accurate choices due to quorum decisions (Ward et al. 2008, 2011). Quorum decisions also play a crucial role for meerkats when coordinating group movement during foraging (Bousquet et al. 2011). The notion that recruitment partly facilitates collective decisions regarding how to react to the current threat of predation is supported by the results of our presentation experiments. However, additional experiments manipulating recruitment and information transfer are needed to generate firm evidence.

The amount of urine may be a potential indicator of predator size and affect prey response. However, the large variation within individuals and between sexes, for example, due to differences in marking behavior (Hart 1974; Jorgenson et al. 1978; Natoli 1985) might make it more difficult for prey species to correctly assess predator size based on the quantity of urine used in deposits. Furthermore, enhanced predator size might not always be the best indicator of danger for meerkats as observations suggest that medium-sized terrestrial predators, such as jackals, are 1 of the main terrestrial predators of meerkats (Clutton-Brock et al. 1999a). Meerkats, being small animals with a body mass of less than 1 kg, fit much better in the prey range of medium-sized predators than larger predators. Thus, meerkats may not benefit from discriminating different quantities of dog urine, and hence did not increase vigilance when presented with magnified cue quantities.

Table 3
Model selection process for (a) vigilance of recruited individuals and (b) latency to resume foraging

	AIC
(a) Vigilance of recruited individuals	
Age of urine + number of animals recruited + amount of urine	82.48
Age of urine + number of animals recruited	**80.82**
Age of urine	89.95
Number of animals recruited	92.23
(b) Latency to resume foraging	
Age of urine + number of animals recruited + amount of urine	**149.4**
Age of urine + number of animals recruited	150.1
Age of urine + amount of urine	164.8
Number of animals recruited + amount urine	151.6

Final models with the lowest AIC (bold) are presented in Table 2.

Predator response

Meerkats responded earlier to the presented moving terrestrial predator in their close vicinity, when being exposed to a DPC that indicated the presence of a terrestrial predator in comparison to a control cue of a herbivore. The latency to emit the first alarm call to the predator was shorter when the meerkats encountered a DPC compared with a control cue. In our experiment, meerkats typically emitted medium to high urgency terrestrial alarm calls referring to terrestrial predators (Manser 2001), when detecting the mounted caracal (Zöttl, personal observations), suggesting that the mounted caracal was identified as a terrestrial predator.

Enhanced predator response due to the decreased latency to alarm in response to the dummy predator may have been caused by (1) an increased sensitivity to the terrestrial predator or (2) a general increased perceived risk, resulting in a higher vigilance after the exposure to the DPC. With our experiment we cannot distinguish between these 2 nonmutually exclusive alternatives. Evidence for increased sensitivity

due to perceived risk or vulnerability on antipredator has been found in the brushtail possum which reacts stronger to a DPC in the absence of shelter (Parsons and Blumstein 2010). It seems likely that increased vigilance during and after recruitment is the key to faster predator detection in meerkats. From our results, we can infer that due to the encounter of odor cues a faster response to the predator by the whole group was achieved. Whether the reduction in latency to alarm to the simulated predator was potentially caused by specific information available to the receiver about the type of danger in the acoustic structure of the recruitment calls, or a general heightened perceived risk due to the DPC and the recruitment calls, needs further experiments. A broad body of literature documents behavioral changes in response to predator odors (Apfelbach et al. 2005), and numerous authors assume that animals increase their survival rates by reacting to DPCs (Berger et al. 2001; Brown et al. 2004; Monclus et al. 2005; Ferrari et al. 2006; Templeton and Greene 2007; Blumstein et al. 2008; Roth et al. 2008; Lohrey et al. 2009; Webb et al. 2010). However, our study provides the first experimental evidence showing a faster response, likely due to faster detection of a predator, which might help to increase survival (Fitzgibbon 1989; Krause and Godin 1996; Lingle and Wilson 2001) after recruitment to DPCs.

The individual that recruited the group to the DPC was not always the first to give the alarm call in response to the dummy predator, suggesting that individuals benefit from recruitment rather than from the DPC encounter per se. Likely, the individual encountering the cue may be at the greatest risk to be close to the predator, if it is still in the area. By recruiting others to the spot, it dilutes the risk of being predated (Foster and Treherne 1981; Uetz and Hieber 1994; Roberts 1996), and several together, may be able to deter the predator (Lingle 2001; Graw and Manser 2007). This would directly benefit the caller, but may not fully explain why the other group members should interrupt foraging. Rather, the additional observation that it was rarely the individual closest to the predator that gave the initial alarm call indicates that recruiting group members enables information transfer and as a consequence every individual is aware of the magnified predation risk. This may allow the costs of antipredator behavior to be shared among group members, which likely benefits all of them including the recruiter.

CONCLUSIONS

We show that meerkats interrupted foraging and were more likely to spot a predator during this interruption, whereby they attended to specific qualities of the cue, that is, more to the age than the quantity of the cue. Age is likely a more reliable indicator about the immediate risk of the situation than the quantity, which may be affected by many other factors. To fully understand costs and benefits involved in recruitment calling, further research is needed to disentangle whether recruitment is a selfish behavior from both the recruiter and the recruited individual that results in a coordinated action, or whether it is a cooperative behavior incurring net costs to one of the involved parties.

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